

12.

Factors Influencing the Establishment of Residence in Shells by
Tropical Shore Fishes.

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(Plates I & II; Text-figures 1-5).

INTRODUCTION.

A considerable variety of small tropical shore fishes establish more or less permanent residence in empty shells or similar cavities. Many maintain a proprietary attitude toward the territory immediately surrounding their place of abode, and not infrequently modify their area of activity by excavational or other means. Prominent among such shore fishes are *Pomacentrus leucostictus* Muller and Troschel and *Bathygobius soporator* (Cuvier and Valenciennes). Both species are abundant at Bimini where these studies were carried out at the Lerner Marine Laboratory during 1948 and 1949. Reasons were sought for the selective activity of these fishes, their method of recognizing home grounds and the general basic nature of the relationship of the individuals to these elements in their environment with which they have such intimate and continued contact. Both are vigorous in defense of their territories but differ notably in the rhythm of their activities. *Pomacentrus* is strictly diurnal and spends the dark hours completely hidden within the cavity of its selection, as has been indicated by Longley and Hildebrand (1941) and Breder (1948). *Bathygobius* on the other hand is active both during the daylight and dark periods.

In a suitable aquarium both species will accept practically any cavity offered as a place of retreat and after a period of establishment will defend their territory, which usually includes the whole aquarium floor, against all comers. For this reason the number that may be successfully kept in a small aquarium is sharply restricted because of fighting which frequently results, especially in the case of *Pomacentrus*, in the death of all but the dominant fish.

Although not closely related, there are many points of resemblance in the behavior of these two species. For example in modifying their environment both will excavate sand by fanning it away with their tails. *Pomacentrus* will often "fan" away marauding small invertebrates with more or less success while *Bathygobius* is more given to direct oral attack under similar conditions. Both will at times evince very definite reac-

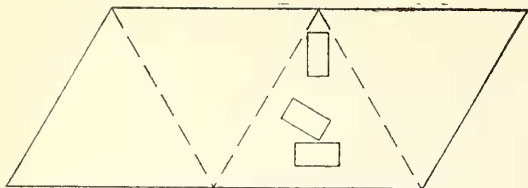
tions to an object moved from its accustomed place and if it is possible *Pomacentrus* will often return it repeatedly to its original site. This behavior was very well demonstrated in one aquarium containing a single mature *Pomacentrus*. A glass tube attached to a flexible rubber tube fed water to the aquarium and rested diagonally across the tank with its end resting on the bottom. If this tube was moved from a certain position it was always returned to it by the fish, frequently immediately, but always in at least 15 minutes. The fish would swim around the tube as though "studying" the situation and finally press its mouth against the tube and swim vigorously, replacing the tube to a position against one wall of the aquarium. This was close to the limits of physical ability of the fish and not infrequently as many as three separate attacks were necessary to replace the tube to the "desired" spot.

With material showing behavior as above outlined it would be expected that some of the reactions would be found to be fairly complex. The present contribution is to be considered an initial attempt to distinguish some of the elements comprising these reactions.

EXPERIMENTAL PROCEDURES.

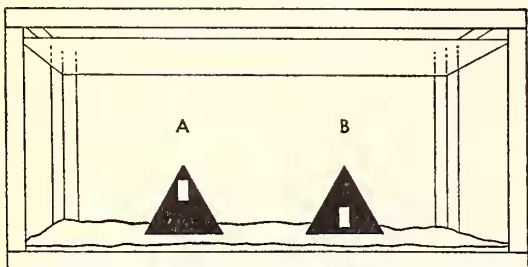
Since the shells inhabited by these fishes (most often *Strombus*) are fairly complicated forms in a physical sense it was thought that perhaps a simplifying of the form of the shelter would make it possible to understand more clearly the basic nature of some of the behavior. To this end a number of tetrahedrons were made of cardboard with a suitable opening as shown in Text-fig. 1. Some were prepared of black cardboard and some of white. With these as the only fittings in the aquaria, which measured 2' × 1' × 1', the following experiments were undertaken.

Experiment 1. Two newly caught *Pomacentrus* about 1 inch in length and as nearly identical in coloration as possible were placed in an aquarium with two black tetrahedrons as shown in Text-fig. 2 on August 2. One fish discovered the opening in "B" in about five minutes but did not enter, simply hovering



TEXT-FIG. 1. Pattern for the cardboard tetrahedrons. Three openings are indicated, only one of which was used in any one shelter. The altitude of each triangular face is 4 inches. The cut edges were bound with transparent Scotch tape.

about and "examining" it. In these black tetrahedrons the opening becomes nearly invisible since the surface reflection of the cardboard largely disappears under water, except for the following condition in tetrahedron "B." Both had a small quantity of sand placed in them in order to insure their stability. Thus the one with the lower hole showed white through the opening while "A" with the upper hole did not. After about 20 minutes the fish entered "B" and seemed to accept and take possession of it. The other individual hovered about "A" at this time but evidently had not found the entrance.

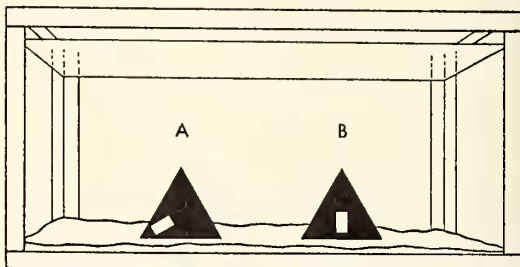


TEXT-FIG. 2. First arrangement of tetrahedrons in experiment 1.

One hour later the fish which established itself in "B" found the entrance in "A" and took possession of this as well. By now it was clear that this fish was definitely dominant over the other, which was not permitted near either of the tetrahedrons. The general situation at this time is shown in Plate I, Fig. 1. This condition was continued through the following day with no change of status. On the third day the tetrahedron "A" was changed in position as indicated in Text-fig. 3. While this change was being made the resident fish hid in "B" and as a consequence could not see the shift of position. Because of the nature of the geometrical figure used the only optically detectable change would be that of the place of the entrance. When the resident came out of "B" it swam to the place of the entrance of "A" before the shift. It momentarily stood there and then fled to hide in "B" again. In a short time it emerged and in about five minutes it found the new place of the entrance and from then on used it freely as shown in Plate I, Fig. 2. This continued for five days after which the experi-

ment was terminated. Although these fish used these cardboard boxes freely, as described, on the coming of nightfall they would leave them and spend the night resting in the corners of the aquarium. A shell, on the other hand, is always occupied at night.

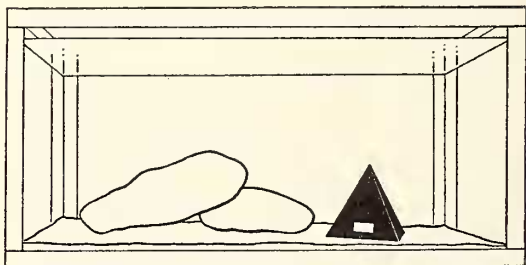
Experiment 2. On August 4, with two new but similar-sized *Pomacentrus*, another aquarium was set up with one black tetrahedron as in "A" of experiment 1 but with a small *Strombus* shell in place of "B." This



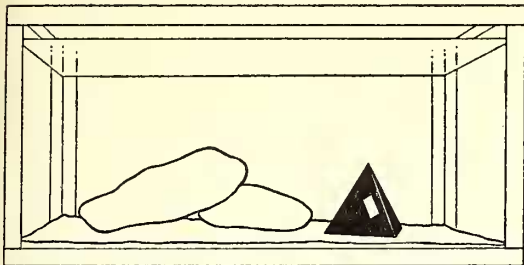
TEXT-FIG. 3. Second arrangement of tetrahedrons in experiment 1.

was maintained for four days and neither fish paid the slightest attention to the tetrahedron. The dominant fish occupied the shell and the other rested in aquarium corners.

Experiment 3. One black tetrahedron was placed in another aquarium with two pieces of beach rock disposed so that one leaned on the other as indicated in Text-fig. 4. In this aquarium on August 12 were placed two *Pomacentrus*, two *Bathygobius* and four small *Sparisoma* sp. One *Bathygobius* immediately "inspected" the tetrahedron but did not enter. A few minutes later a *Pomacentrus* did the same. By three-quarters of an hour it was occupied by a *Bathygobius* which sat in the entrance with the head out as shown in Plate I, Fig. 3. The following day the same condition prevailed but when the goby was out of the tetrahedron it was visited by several of the scarids. One finally prevented the others from entering but the goby repossessed the place in a short time. On the fourth day the tetrahedron was turned as in Text-fig. 5. The goby which had been occupying it did not immediately find the entrance but clung with its ventral sucker to the place where the entrance had formerly been located. In



TEXT-FIG. 4. First arrangement of tetrahedron in experiment 3.



TEXT-FIG. 5. Second arrangement of tetrahedron in experiment 3.

about one-half hour the new location of the entrance was located and the goby balanced itself on the cardboard edge with its head out. The other fishes had to content themselves with finding shelter under the beach rock. As with the other experiments this tetrahedron was not used after dark, but on one occasion the *Bathygobius* entered it after a flashlight was played on the aquarium for some time. This experiment was discontinued after five days.

Experiment 4. One black and one white tetrahedron were placed in an aquarium on August 17 as in experiment 1 but with both openings as in the start of experiment 3. Two new small *Pomacentrus* were placed in the aquarium. Neither shelter was seen to be entered until the third day, when one fish dominated the entire situation and entered both freely, but "lived" in the white one. The behavior was otherwise very like experiment 1. The other fish was completely subjugated and both spent the night out of the tetrahedrons. This experiment was terminated on the fifth day.

As far as these preliminary experiments go they tend to indicate that such forms of cardboard are acceptable, but not for use at night, that the entrances are memorized as to location, that light-colored retreats are preferred over dark and that all cavities within the area of one fish's domination are defended. Because of the refusal to accept the cardboard tetrahedrons at night, similar ones were constructed of concrete of identical external dimensions but slightly smaller inside because of the necessary thickness of the walls which were about one-quarter inch. Using these, the following series of experiments was undertaken.

Experiment 5. Two concrete tetrahedrons, painted white, were arranged essentially as in Text-fig. 2 but with both openings at the bottom. On January 2 at 3:00 p.m. two newly caught *Bathygobius* as nearly identical as possible were introduced. By 4:00 p.m. one had become dominant and was occupying the right-hand shelter. In another hour it occupied both alternately and the subjected individual remained in a corner of the aquarium. The next day each fish occupied a shelter, where they remained most of the time. There was no evidence of quarreling. There seemed to be no peck order. This behavior con-

tinued unchanged and on January 16 an empty conch shell was placed midway between the two shelters. There was immediate investigation by both fish but no entry into the shell was observed, as shown in Plate II, Fig. 1. No further changes were made in this aquarium and the fishes spent less and less time in the shelters so that by March 24 the doorways had become so overgrown with a filamentous algae as to completely block entry. If the fishes had forced their way through it when not observed, evidence of their entry would have been noticeable. Also by this time the fish had become so tame that if one placed a finger in the tank they would come to the surface and bite it. On March 27 one goby was in the "dominant" color phase and was mildly chasing the other. The difference in pattern has been discussed by Breder (1949) and illustrated in Plate II, Fig. 1.

Experiment 6. On January 3 an experiment was established identical with experiment 5 but with different individuals. The same day these fish established a peaceful relationship, each occupying a shelter as shown in Plate II, Fig. 2. The fish disappeared the next day, evidently having jumped out of the tank.

Experiment 7. The physical arrangements were as in experiments 5 and 6 but with one small *Pomacentrus leucostictus* and one small *P. adustus* Troschel as near the same size as possible. These were introduced at 6:00 p.m., January 3. There was no immediate entry but by nightfall one fish was found in each shelter. The next day it was apparent that the *P. leucostictus* was dominant over the other fish as was evidenced by the chasing, although both were in "possession" of their separate shelters. On January 11 an additional shelter was placed between the two tetrahedrons. It consisted of two small slabs of concrete standing on edge in the sand and a top of a similar slab on its side. Investigation by both fish was prompt and thorough. The conditions were unchanged by January 16 and there was little chasing or molestation. After an absence from the laboratory it was found on March 24 that only the *P. leucostictus* was present and it used the concrete slabs for shelter. On March 27 it used the shelter formerly occupied by the other fish.

Experiment 8. An aquarium was provided with one white tetrahedron and one conch shell. On January 3, two similar *Bathygobius* of about 70 mm. were introduced. Both shell and shelter were frequented the next day by what was evidently the dominant fish. The shelter was used first. Two small *Pomacentrus leucostictus* of about 10 mm. were added. Both gobies immediately chased them about and prevented entry into shell or shelter. The next day one *Pomacentrus* was dead. The other now occupied the shelter while its former occupant hid in a corner. It is to be noted that in both species the tetrahedron was used first. The next day at 8:15 a.m. the goby was in the shelter while

the *Pomacentrus* was out foraging and evidently unconcerned about the goby. By 9:00 a.m. the *Pomacentrus* was back and the goby in the corner. Later in the day the goby was seen to enter the shelter while the *Pomacentrus* was foraging again and voluntarily to leave the shelter before the *Pomacentrus* returned. This continued until January 8 when the *Pomacentrus* disappeared. It could have been easily eaten by the goby. This goby now occupied the shell, while the subjugated one had excavated a place under the shell which it occupied. By noon the dominant was back in the shelter and the subjugated back in the shell. Conditions continued in this fashion at least until January 16. After an absence from the laboratory only one goby was found and it sought shelter under the shell, March 24, but on March 28 it was back in the concrete shelter.

Experiment 9. Here the arrangement consisted of a red and a green tetrahedron and two *Pomacentrus leucostictus* almost too large to pass through openings in shelters established on January 8. One fish used the red shelter and the other hid in a corner. The next day one fish was in each shelter, and at 9:00 p.m. on the following day one was found in the red and none in the green, with the situation reversed at 10:00 p.m. The subjugated fish, whose fins had been damaged, was removed to another aquarium. The remaining fish from then on was in and out of both shelters. On January 16 two more shelters were added, one white and one black. There was no entry of these new shelters; the fish alternated between the two already present as shown in Plate II, Fig. 3. By March 24 the fish had become very tame and was seen on occasion to go into the green shelter, which was just barely possible because of the growth of the fish in the intervening time. Colors of tetrahedrons had become much reduced because of a growth of algal scum.

Experiment 10. An aquarium was arranged as in experiments 5 and 6, that is, with two white tetrahedrons. One *Pomacentrus* was introduced on January 10. This was the subjugated fish from experiment 9. It used both shelters indifferently, up to January 16 when a conch shell was placed between the two shelters. The fish hid in one of the shelters for a long time. After interruption in the observations because of an absence from the laboratory it was found that the fish was using the shell for residence on March 24. This may have had to do with the size of the opening and growth of the fish. There was no interfering algal growth in this tank.

In all these experiments with the concrete shelters the *Pomacentrus* stayed inside all night, as they do with shells.

DISCUSSION.

The preceding experiments represent observations covering 421 tank days on the reactions of 26 individual fishes in respect to shelters and companions. The individual experiments ranged from 1 to 85 days in

length with a mean length of 42.1 days. The details may be conveniently shown by the following tabulation.

EXPERIMENTS AND NUMBER	LENGTH IN DAYS		
	MINIMUM	MEAN	MAXIMUM
4 with cardboard shelters	4	4.75	5
6 with concrete shelters	1	67.0	85
Total of 10	1	42.1	85

SPECIES INVOLVED	NUMBERS OF INDIVIDUALS USED		
	CARD-BOARD	CONCRETE	BOTH
<i>Bathygobius soporator</i>	2	6	8
<i>Pomacentrus leucostictus</i>	8	5	13
<i>Pomacentrus adustus</i>	—	1	1
<i>Sparisoma</i> sp.	4	—	4
Totals	14	12	26

Since the series of experiments with cardboard shelters was carried out in August and those with concrete in January to March, a difference in water temperature in the aquaria existed, as given below.

SEASON OF OPERATION	WATER TEMPERATURE °C.		
	MINIMUM	MEAN	MAXIMUM
August 2-20	29.0	30.1+	31.5
January 2 to March 28	20.0	24.2—	27.0

With these data and various general considerations it is possible to arrive at certain preliminary conclusions that should be basic to further, more detailed study of the behavior of these fishes by more refined and analytical techniques.

It is evident from all of these experiments and other observations that a dominant fish takes over the whole tank area and volume, defending all manner of shelters and shells. The evidently less desirable corners of the aquarium may or may not be left to the subjugated fish. This is in agreement with the earlier studies using more individuals and a larger variety of species (Breder, 1948). Incidental observations on similar fishes which became established in larger concrete tanks measuring 6' × 3' × 2' deep showed that under such conditions an individual of either species might establish a territory of about half the bottom area of such a tank, or approximately 9 square feet. Observations in tide pools show a somewhat similar area for fishes of comparable size while those on open sandy beaches have been observed to control an area of a radius not more than 2 feet, which is equivalent to an area of approximately 12.5 square feet. Adults of *Pomacentrus leucostictus* generally do not defend an area with a radius of much over 3 feet or an area of approximately 28 square feet.

Although it is not indicated in the preceding remarks, it was clear during the summer tests in the experimental aquaria, as well as in numerous others, that there was much more fighting and chasing at that time than during the winter tests. This difference is evidently related to the difference in temperature of the water, 30.1° versus 24.2°, as well as perhaps the very slightly longer daylight periods in summer at this latitude. Re-

productive tendencies may also have influenced the gobies but such influences could not be present in the *Pomacentrus*, as they were immature.

As is obvious from the most casual observations, these experiments confirm the fact that both species under discussion are acutely aware of the physical features of their environment. They both spend much time swimming around and nosing into crevices of any new object or one which has been turned around or otherwise disturbed. As was noted by Breder (1949), they also will not infrequently return an object to its original site if they are capable of moving it. *Bathygobius* generally perches itself on the new object after it has "inspected" it for a time, perhaps obtaining further sensory data through the pelvic sucker. *Pomacentrus* on the other hand seldom touches such objects. As is indicated by the results of experiments number 5, 7, 9 and 10, these fishes show a considerable reluctance to adopt a new shelter once they are well established in old ones.

Pomacentrus will spend the dark hours in a shell or a concrete shelter, but will not so use a cardboard one, seeking instead, if only such is present, a corner of the aquarium. This fact would seem to indicate that a solid and firm structure free from vibration or other movement is sought for passing the night. When vision is possible, as in the daytime, this requirement is evidently less important although, as indicated by experiment 2, a shell is chosen as against a cardboard shelter while, as shown by experiments 5, 7, 9 and 10, no such selection is evident between shell and concrete shelter. This is the more notable because surely none of the fishes used ever had any prior experience with a shelter even approximating the form of a tetrahedron. Similar observations could not be made on *Bathygobius* for they are found both in and out of shelters by day or night, apparently being nearly aperiodic in habits. In experiment 3, however, they seemed to prefer the shelter of a cardboard tetrahedron over the more open shelter of rounded rocks.

There is no evidence from any of the 10 experiments that could be used to indicate any clear color preference in either the cardboard or concrete shelters. Evidently if there is any, it is of an order of magnitude too small to be made evident by these means.

Long residence in an aquarium evidently makes for less use of the shelters. Such behavior was especially marked in experiment 5 where shelters were completely abandoned. After some two months the entrances of the shelters were completely blocked by a dense growth of filamentous algae. There is nothing especially notable about this except the completeness of its nature. Anyone who has had long experience with fishes in captivity knows that the behavior of long resident fishes is often strikingly different from that of newly introduced individuals even long after the initial shock period has passed.

That *Pomacentrus* small enough to be swallowed by larger *Bathygobius* may attain a dominant position is in keeping with observations on other fishes that have a pronounced territorial behavior. For example, this is especially notable among nesting male fresh-water centrarchids as was indicated by Breder (1936).

SUMMARY.

1. In the small areas of 2 square feet, provided by the aquaria employed, the dominant individual of both young *Pomacentrus leucostictus* and *Bathygobius soporator* defended all shelters and shells, leaving only the evidently less desirable aquarium corners for the subjugated individual and sometimes not even those. In nature an area of more than 12 square feet may be defended.

2. Once these species have become established, it evidently takes some time for them to recognize a change in the location of the entrance to a shelter, since they repeatedly go to the site of the original entrance.

3. Cardboard shelters, while used during the daytime, are not used at night by *Pomacentrus*, but nights are passed in similar concrete shelters. This is indeterminate for *Bathygobius* since its behavior is nearly aperiodic. Evidently the solidity and rigidity of concrete and shell as compared with cardboard is a factor in this differential behavior.

4. A shell is preferred to a cardboard shelter, but no such preference could be detected between a concrete shelter and a shell.

5. If there is any color preference for such shelters it is not evident from these experiments and is therefore presumably a factor of small or no consequence.

6. Long residence in an aquarium evidently makes for less use of shelters, leading to complete abandonment of their use in one case of two *Bathygobius*.

7. *Pomacentrus* small enough to be swallowed by *Bathygobius* may nevertheless establish dominance over the latter for a time at least.

8. When these species are well established in an aquarium and accustomed to certain shelters, they have always been seen to elaborately "inspect" any newly introduced shelter, although they may be very reluctant to use it.

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EXPLANATION OF THE PLATES.**PLATE I. Cardboard shelters.**

- FIG. 1. Experiment 1 showing dominant fish in right-hand shelter and the other in the background.
- FIG. 2. Experiment 1 showing dominant fish in left-hand shelter after it had found the changed position of the opening; the other fish, not shown, is hiding in a corner.
- FIG. 3. Experiment 3 showing dominant fish in entrance of shelter; others, not shown, are hidden under and behind rocks.

PLATE II. Concrete shelters.

- FIG. 1. Experiment 5 showing both fish out of the shelters, the dominant (note pattern) perched on the newly introduced shell.
- FIG. 2. Experiment 6 showing two fish each occupying a shelter.
- FIG. 3. Experiment 9 showing the single fish occupying the green shelter. It is far back in the shelter, a condition made necessary by its large size. The red shelter is on the right and the black and white in the rear.